ETHOLOGY OF *NEOCERDISTUS ACUTANGULATUS* (DIPTERA: ASILIDAE) IN SOUTH AUSTRALIA^{1,2}

ROBERT J. LAVIGNE

Entomology Section, University of Wyoming, Box 3354, University Station, Laramie, Wyoming 82071.

Abstract.—A field study of the ethology of *Neocerdistus acutangulatus* in South Australia revealed the following facts. Prey taken by *N. acutangulatus* represented seven insect Orders, suggesting opportunistic euryphagy, although both sexes showed a predilection for Diptera. Mating, without prior courtship, took place in the tail-to-tail position. Eggs were deposited singly in the soil.

The present paper is the third in a series dealing with the ethology of South Australian robber flies. The first paper dealt with *Neoitamus vittipes* (Macquart) (Lavigne, 1982a) and the second with *Neoscleropogon elongatus* (Macquart) (Lavigne, 1982b).

While on sabbatical at the Waite Agricultural Research Institute (November 1978–May 1979), I investigated the behavior of *Neocerdistus acutangulatus* (Macquart) in a horse paddock owned by L. Walter, one km east of One Tree Hill, SA during the period April 5 to 30, 1979. One Tree Hill is a small village, east of Elizabeth, near Para Wirra National Park.

Published records of the occurrence of *Neocerdistus acutangulatus* are few. Macquart (1847), describing it in the genus *Asilus*, gave for the locality both "Nouvelle-Hollande" and "Tasmanie." For some reason Hardy changed the spelling of the species name in 1926 so that it read *acutangularis*. He retained this misspelling in his later papers and the error has been repeated in subsequent literature. In the same paper Hardy (1926), established *Neoitamus abditus* White as a synonym: "There is no species from Tasmania that fits Macquart's description so well as White's *N. abditus*, so there can be little doubt concerning the correctness of this synonymy." On this basis, Hardy provided the following distribution: "Tasmania, Victoria and New South Wales, February to April." In a later paper (1935) however, he stated "It is possible that there is more than one species incorporated under this name the name, however, is generally applied to the Tasmanian form, which also occurs in the vicinity of Melbourne. If the name be applicable to a species from New South Wales, and that may possibly be distinct,

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Fig. 1. Horse paddock, one km east of One Tree Hill, SA, in which a population of *Neocerdistus acutangulatus* was studied.

it will be necessary to revert to White's specific name for the present form." The species whose behavior is described in this paper was identified by Mr. Gregory Daniels, the current authority on Australian Asilidae.

In addition to the South Australian population, on which this paper is based, the author, during a trip to Canberra, ACT and return, collected the species 5.4 km SW of Stawell, Victoria in the Grampians (10.iv.79) and in Back Street State Forest, 19 km east of West Wyalong, NSW (14.iv.79). The Grampians population existed in a habitat similar to that described for the South Australian population. In Back Street State Forest, the asilids were observed foraging from leaves and dead limbs of *Acacia* sp. and *Eucalyptus* sp. at heights up to three meters.

The dominant vegetation in the SA horse paddock was *Eucalyptus fasciculosa* F. Muell. (pink gum) with an understory of grass, primarily *Stipa* sp. and *Pentaschistis thunbergii* (Kunth) Stapf, a bunch grass. Occasional patches of the shrub, *Daviesia ulicina* Sm. were present in the area (Fig. 1).

The paddock was triangular, encompassing a fenced area of 30.5 km^2 . Based on observations made on random transects, the population of asilids was estimated to be 75 to 100 individuals. The sex ratio (\bar{x} 1:1) was obtained intermittently throughout the study by counting males and females observed during standardized time periods. Males dominated the population in early April, whereas females tended to dominate in late April.

The population was widely distributed although there appeared to be a greater density of asilids on and along a riding path which intersected the paddock. With the exception of activity associated with oviposition, almost all (88%) actions performed by N. acutangulatus were initiated on the surface of strips of fallen *Eucalyptus* bark.

The period during which adult asilids could engage in their behavioral patterns was most certainly constrained by factors of weather. On five of the 11 days the site was visited, there was rain in the morning hours (before 1000 h). On three additional days the morning sky was overcast, but cleared later in the day; however, on one of these days it began to rain about 1700 h. Some days there would be intermittent rain showers. Temperatures on site during periods of observation ranged from a high of 30°C (6.iv.79) to a low of 17°C (27.iv.79).

METHODS

Methods for gathering and analyzing ethological data on *N. acutangulatus* were the same as those described for *Neoitamus vittipes* (Macquart) in Lavigne (1982a).

FORAGING AND FEEDING

Perch sites, from which *N. acutangulatus* launched attacks on potential prey, were somewhat variable. Sand, surface debris, broken branches, and fallen *Eucalyptus* bark were all utilized; however, as indicated earlier most activities were initiated from fallen *Eucalyptus* bark. Exclusive of soil surface, heights where foraging individuals were observed varied from 15 to 61 cm.

All forage flights were directed at insects that were airborne, and varied in distance from 13 to 61 cm. While attempting forage flights, this species often became entangled in the vertical vegetation, primarily grass and thus failed to catch prey. Obviously the strategy of using large pieces of *Eucalyptus* bark, while excellent for mating purposes, reduces changes for prey capture since asilids must sometimes fly up through the vegetation to reach potential prey. Conversely, bibionid flies which comprised 20% of this asilid's diet, also used the bark as landing sites, thus making them particularly vulnerable. Curculionid beetles, with open elytra in flight, also were very vulnerable because of their slowness; these small beetles constituted an additional 15% of the diet of *N. acutangulatus*.

In all instances where feeding asilids were watched for extended periods of time, prey were manipulated at least once. Of the 12 feedings, 42% of the prey were manipulated once, 42%, twice and 16%, three times. Manipulation consisted of the asilid raising the anterior portion of the body, resting the apex of the fore and middle femora on the substrate and utilizing these same tarsi to change the position of the prey prior to reimpaling it. The hind legs were always used as stabilizers and to maintain position (Fig. 2). During feeding, soft bodied prey balloon, which is related to the injection of proteolytic enzymes and subsequent food pumping (Lavigne and Holland, 1969; Musso, 1968).

In the single instance where an entire feeding was recorded, the female landed with a tiny curculionid beetle impaled, following a 61 cm forage flight at 1426 h. Two minutes later, the beetle was manipulated and reimpaled on the asilid's proboscis. During the period 1435–1440 h, the asilid was harrassed several times by tiny black ants. Each time she would fly into the air, but would land again on the same piece of *Eucalyptus* bark, although at a different location. At one point upon relanding, she cleaned ovipositor, wings and left middle leg in that order. The female defecated at 1445 h and subsequently wiped her ovipositor on bark to clean it. At 1449 h she pushed the prey off her proboscis with her fore tarsi.

Once feeding is completed, the asilid's fore tarsi are used to push the prey's

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Fig. 2. Mated pair of *Neocerdistus acutangulatus* with female manipulating unidentified bibionid (Diptera). Note the use of fore and midtarsi to reposition prey, while hindtarsi are used to maintain position.

Fig. 3. Same mated pair of *Neocerdistus acutangulatus* resting on fallen branch of *Eucalyptus fasciculosa*. Note how repositioned prey is held with the fore tarsi. Note also vertical position of male claspers encircling female's ovipositor.

	Predator length (mm)*			I	Prey length (No. prey	Mean ratio of predator;	
Sex	Min.	Max.	Mean	Min.	Max.	Mean	measured	prey
Male	8	11	9.5	1	6	2.96	51	3.2
Female	9.25	12.25	11.1	1	7	3.73	85	3.0
Combined	8	12.5	10.5	1	7	3.44	136	3.05

Table 1. Relation between length of Neocerdistus acutangulatus and that of its prey.

* 10 predators of each sex were measured from the One Tree Hill population.

exoskeleton off of its proboscis. Of 28 prey discards observed, 50% were accomplished on the feeding site, while the remainder occurred as the asilid flew, often during pursuit of a new prey item. In one instance, the asilid was observed to hover 7.5 cm from the feeding site while pushing the prey off its proboscis.

PREY SELECTION

Based on 136 measured prey, the "preferred" prey length was 3.44 mm, although the prey varied from 1 to 7 mm. Females were slightly larger than males (11.1 vs 9.5 mm) and captured, on the average, slightly larger prey (3.73 vs 2.96 mm) (Table 1). The mean predator to prey ratio for this species was 3.05, very close to that (2.9) for *Neoitamus vittipes* (Lavigne, 1982a). *N. vittipes*, while slightly larger (\bar{x} 12.1 mm) than *N. acutangulatus*, also takes slightly larger prey (\bar{x} 4.2 mm).

While males captured representatives of five Orders, females took representatives of seven Orders, indicating that this species is euryphagic, as defined by Lavigne and Holland (1969). The most intense predation by both sexes, however, was on members of the Order Diptera (Table 2). This predilection for Diptera is shared in somewhat greater degree by at least three species of *Neoitamus* (Lavigne, 1982a). Although only approximately 20 insect families are included among the array of prey, it is suspected that this asilid species is opportunistic, attacking those prey existing in the same microhabitat, when they fly within view of the asilid. There was no evidence of cannibalism in this species. Since the same landing sites are used continuously, it was not to be expected.

Here follows a list of prey taken by *N. acutangulatus*. Specific identifications were made where possible, but because of the primitive state of taxonomy in some groups, definitive identification was often impossible. "It is probably not realized by many people that about 40% of Australia's insect fauna is still undescribed, adding further difficulties to the determination of specimens" (Murray S. Upton, CSIRO, Manager, Australian National Insect Collection—Pers. Commun.). The number of records and sex of the predator are indicated in parentheses following the prey record. The collected prey are housed at Waite Agricultural Research Institute, Adelaide, South Australia.

COLEOPTERA, Curculionidae: undet., 19.iv.79 (δ , 2 \circ), 20.iv.79 (2 δ , 5 \circ), 23.iv.79 (2 \circ), 24.iv.79 (5 \circ), 26.iv.79 (4 \circ , ?), 27.iv.79 (\circ). DIPTERA, Anthomyiidae: undet., 18.iv.79 (\circ), 19.iv.79 (δ), 23.iv.79 (δ , 2 \circ), 24.iv.79 (\circ), 26.iv.79 (δ); Bibionidae: *Dilophus* sp., 6.iv.79 (4 δ , 8 \circ), 18.iv.79 (2 δ , \circ), 19.iv.79 (δ , 8 \circ), 20.iv.79 (3 δ), 23.iv.79 (\circ), 24.iv.79 (\circ), 24.iv.79 (\circ), 26.iv.79 (δ), 20.iv.79 (δ , 2 \circ); Cecidomyiidae: undet., 19.iv.79 (\circ), 20.iv.79 (δ), 23.iv.79 (δ , 4 \circ), 24.iv.79 (7 δ , \circ), 26.iv.79 (\circ); Chironomidae:

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	Male		Female		Unknown		Total	
Order	No.	%	No.	%	No.	%	No.	%
Coleoptera	3	2	21	13.8	1	0.7	25	16
Diptera	42	27.6	51	33.5	1	0.7	94	62
Hemiptera-Heteroptera			3	2			3	2
Hemiptera-Homoptera	3	2	6	3.8	1	0.7	10	7
Hymenoptera	5	3.3	8	5.2			13	9
Isoptera			5	3.3			5	3
Lepidoptera	1	0.7	1	0.7			2	1
Total	54	35.6	95	62.3	3	2.1	152	100

Table 2. Numbers and percentage of prey of different Orders taken by Neocerdistus acutangulatus.

undet., 23.iv.79 (\hat{v}); Dolichopodidae: undet., 5.iv.79 (\hat{v}); Mycetophilidae: undet., 23.iv.79 (\hat{v}), 24.iv.79 (\hat{v}), 27.iv.79 ($\hat{\delta}$), 30.iv.79 (\hat{v}); Sciaridae: undet., 19.iv.79 ($\hat{\delta}$), 23.iv.79 (\hat{v}), 27.iv.79 ($\hat{\sigma}$), 30.iv.79 (\hat{v}); Sciaridae: undet., 19.iv.79 ($\hat{\delta}$), 23.iv.79 (\hat{v}), 27.iv.79 ($\hat{\sigma}$), 19.iv.79 (\hat{v}), 27.iv.79 (\hat{v}), 27.iv.79 (\hat{v}), 19.iv.79 (\hat{v}), 28.iv.79 (\hat{v}), 30.iv.79 ($\hat{\delta}$); Tipulidae: undet., 23.iv.79 (\hat{v}), 27.iv.79 (\hat{v}), 19.iv.79 (\hat{v}), 28.iv.79 (\hat{v}), HEMIPTERA-HETEROPTERA, Lygaeidae: Nysius sp., 28.iv.79 (\hat{v}), undet., 19.iv.79 (\hat{v}), 28.iv.79 (\hat{v}), 18.iv.79 (\hat{v}), 28.iv.79 (\hat{v}), 28.iv.79 (\hat{v}); Psyllidae: Creiis sp., 18.iv.79 ($\hat{\delta}$), 23.iv.79 (\hat{v}), 24.iv.79 ($\hat{\delta}$), 23.iv.79 (\hat{v}), 28.iv.79 (\hat{v}), undet., 5.iv.79 (\hat{v}), 6.iv.79 ($\hat{\sigma}$), 23.iv.79 (\hat{v}), 24.iv.79 ($\hat{\delta}$), Glycaspis sp., 24.iv.79 (\hat{v}), undet., 5.iv.79 (\hat{v}), 6.iv.79 ($\hat{\sigma}$), 24.iv.79 (\hat{v}), Ponerinae, 5.iv.79 ($\hat{\delta}$); Encyrtidae: Encyrtinae, 23.iv.79 (\hat{v}); Formicidae (winged reproductives); Iridomyrmex sp., 24.iv.79 (\hat{v}), Myrmicinae, 20.iv.79 (\hat{v}); Tiphiidae: Thynninae, 23.iv.79 (\hat{v}), ISOPTERA, Rhinotermitidae (winged reproductives): Heterotermes ferox (Froggatt), 5.iv.79 (\hat{v} , ?), 19.iv.79 ($\hat{2}$, 26.iv.79 ($\hat{2}$), LEPIDOPTERA, Glyphipterigidae: Glyphipteryx anaclastis Meyrick, 23.iv.79 (\hat{v}), 26.iv.79 ($\hat{\delta}$).

MATING

Strategies used by *N. acutangulatus* to ensure survival of the species did not differ markedly from those exhibited by *Neoitamus vittipes* (Lavigne, 1982a).

No formalized courtship was exhibited by males. Upon observing a female, the male initiates a short flight which puts him in contact with her. The following description of a mating is typical of those observed.

- 10:39 Male resting on fallen *Eucalyptus* bark; female flew in and landed 20 cm distant; male immediately flew towards her and landed on her dorsum; copulation ensued in male atop female position; after 15 seconds the pair took the tail-to-tail position (Fig. 3).
- 10:42 Female cleaned eyes and fore tarsi.
- 10:45 Cleaning activity was repeated.
- 10:53 Male buzzed wings, lifted off surface, disengaged genitalia and flew 15 cm away, landing on the same strip of bark; female remained stationary.

Of the 63 mated pairs observed, only six occurred on a substrate (sand, tree roots and broken branches) other than fallen *Eucalyptus* bark. Two of these pairs were resting in sunlight on tree trunks at heights of $1\frac{1}{3}$ m and $1\frac{2}{3}$ m in late afternoon. Probably they were responding to increasing shade encroachment re-

sulting from the changing angle of the sun's rays as do *Cyrtopogon auratus* Cole adults that spend the night in the tree canopy (Lavigne, 1970).

Males fly from one strip of fallen bark to another in apparent searching flights. When a male lands on a site supporting a female, the female usually reacts almost immediately and flies a straight line distance with the male in pursuit. An immediate response is not always elicited and the male may either fly and land on the resting female or wait until she initiates a forage flight before pursuing her. If the site is occupied by a male, a male-to-male encounter occurs as the other male is landing. The two males occasionally make contact, the faster one landing atop the other and exhibiting copulatory movements. Usually, however, they fly in different directions upon approaching each other closely. Landing males are apparently mistaken for females by other males and the subsequent flight pattern serves to identify the individual's sex.

Pairs were observed in copula as early as 1037 h and as late as 1631 h. The majority of pairs (76%), however, were seen between 1300 h and 1530 h. Temperatures taken on the sites where mated pairs were resting ranged from 19 to 30° C (\bar{x} 23.5°C).

As previously mentioned, once copulation took place in the male over female position, only a few seconds (10–20) elapsed before the tail-to-tail position was achieved (Fig. 3). Five complete matings were observed with the following elapsed times: 8, 9, 12, 12, 14 minutes. Separation occurs when the male releases his claspers and flies away.

Of the 63 mated pairs, 11 females (17.5%) were feeding on prey when observed. Both individuals remained quiet throughout except for prey manipulation and/ or cleaning activity by females.

On two occasions mated pairs were accosted by a second male. The male would fly in, land atop the female and attempt to copulate. The strategy behind such an apparently useless act had always eluded me until I made the following observation. This involved an eight minute "complete" mating. A second male landed two cm in front of a mated male and then flew at the mated pair. The "startled" mated male released his claspers and flew. As he did so, the intruding male landed atop the female and copulated with her. Obviously, sexual harassment sometimes provides a competitive advantage and this may be especially important when populations are small and females are at a premium.

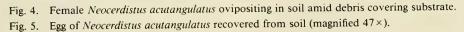
Interestingly enough, once this copulatory act was completed the same female only remained unmated for an additional three minutes before a third male made contact, which resulted in copulation. This pair was startled by a galloping horse and flew out of the observer's sight. This species, like some other species lacking courtship (Bullington and Lavigne, 1980; Lavigne et al., 1980), utilizes multiple mating.

OVIPOSITION

No published records exist concerning oviposition behavior nor have eggs of any members of the genus *Neocerdistus* been described.

The process by which *N. acutangulatus* oviposits is as follows. The female lands on soil directly or on debris covered soil. She then moves her ovipositor laterally back and forth "testing" the substrate. If the substrate is unsuitable, the asilid will move 1-2 cm and repeat the motions. Once a suitable site is located, probably





cracks in the soil, the ovipositor is forced into the substrate with lateral motions (Fig. 4). Based on two egg recoveries, there is apparently only one egg deposited at each site. After 40 to 65 seconds, the ovipositor is removed. While removing the ovipositor, the female brings it between her hind legs and in a series of sweeping motions pushes dirt into the hole, thus ensuring that the egg is covered. At the tip of the ovipositor are two short dorsal-ventrally flattened cerci which aid in

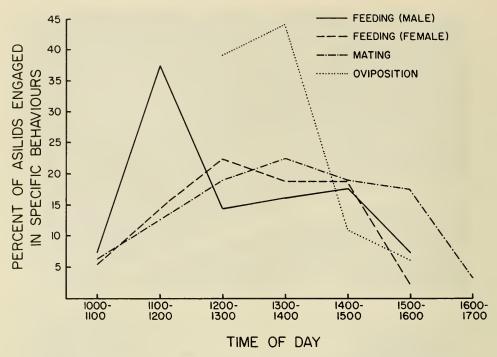


Fig. 6. Mean diurnal rhythm of activity for *Neocerdistus acutangulatus* one km east of One Tree Hill, SA. Percentage of asilids engaged in specific behavior patterns was calculated from the total number of observations for each behavior; i.e. 146 feeding observations, 63 mating observations and 18 observations of ovipositing females.

moving the particles of soil. This structure is similar to that seen on the ovipositor of *Efferia helenae* (Bromley) which also sweeps dirt into the hole following oviposition (Lavigne and Holland, 1969).

Single females were followed after having been observed ovipositing. Each followed female made two more oviposition attempts before I lost sight of them. At each oviposition site I would place a 2 dram vial. Once the female was lost to sight, I would return, place the mouth of the vial over what was assumed to be the oviposition hole and press downwards. Soil and debris would be forced up into the vial; it would be inverted and 70% ethanol would be added and the vial was then corked. The solution thus formed was subsequently examined in the laboratory for the presence of eggs. A more reliable but considerably more time consuming method is to use an empty metal frozen juice container instead of a vial, thus increasing the amount of soil collected and thereby decreasing the chance that the oviposition hole was missed.

Several females were observed exhibiting oviposition behavior around the edge of a large (1 by 3 m) depression, which apparently retained water at certain times. Substrate surface temperatures where ovipositing females (N = 13) were observed ranged from 21 to 33.5°C (\bar{x} 27.4°C).

The earliest oviposition was observed at 1220 h and the latest at 1507 h. With three exceptions, however, all ovipositing females were observed between 1220 h and 1340 h.

Eggs were white when first deposited and retained this color in 70% ethanol. The two recovered eggs measured 0.9 and 1.0 mm long and 0.44 and 0.45 mm wide, respectively (Fig. 5). At a magnification of $70 \times$, there was no visible sculpturing of the chorion. What appeared to be fully mature eggs were dissected from the ovarioles of 3 females that had been observed exhibiting oviposition search movements. These females had been collected and immediately immersed in 70% ethanol. The 69 white dissected eggs measured 0.9–0.98 mm in length (\bar{x} 0.94) and 0.41–0.42 mm in width (\bar{x} 0.41)

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